

## Troidine Swallowtails (Lepidoptera: Papilionidae) in Southeastern Brazil: Natural History and Foodplant Relationships

Keith S. Brown, Jr.<sup>1,2</sup>, Antoni J. Damman<sup>1</sup> and Paul Feeny<sup>1</sup>

<sup>1</sup>Section of Ecology and Systematics, Division of Biological Sciences, Cornell University, Ithaca, New York, 14853, USA and

<sup>2</sup>Departamento de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, C. P. 1170, Campinas, São Paulo, BRAZIL 13.100

**Abstract.** Five species of troidine swallowtails, *Parides proneus*, *P. bunicus*, *P. agavus*, *P. anchises nephalion*, and *Battus polydamas*, sympatric in central São Paulo state, southeastern Brazil, differentially utilize the available *Aristolochia* hostplants. All early stages differ morphologically, with the possible exception of eggs of *P. bunicus* and *P. agavus*. In two study sites, the adult populations fluctuated greatly and disharmoniously in approximate two-month cycles. Individuals moved an average of near 100 m and up to 1.3 km between successive recaptures, probably in search of flower resources. Adult lifespans in the field and laboratory averaged less than two weeks, with a majority of field-recaptured individuals passing through one of the six major wing wear classes per week. Laboratory cultures, maintained in a walk-in growth chamber, were used to investigate larval and adult behavior, pupal diapause, oviposition, and hostplant palatability in the five species of butterflies, with relation to the six potential hostplants sympatric in the field.

### Introduction

Papilionid butterflies in the tribe Troidini have long been known to feed specifically on plants in the genus *Aristolochia*, and are commonly referred to as *Aristolochia* swallowtails. (Rothschild & Jordan, 1906; Munroe, 1960; Ehrlich & Raven, 1964). Although homopterans, tingid bugs, cassidine beetles, and larvae of noctuid and pyralid moths have been observed on *Aristolochia*, relatively few herbivores other than the *Aristolochia* swallowtails can feed on these plants (D'Araujo e Silva *et al.*, 1968; Rausher, 1979a; K. B., pers. obs.). *Aristolochia* vines characteristically contain aristolochic acids (nitrophenanthrenes) that have pharmacological effects on vertebrates (Hoehne, 1942: 14-17; von Euw *et al.*, 1968) and strongly inhibit feeding by some insects (Bernays & Chapman, 1977; Rausher, 1979a). The plants also contain several benzyloisoquinoline alkaloids, sesquiterpenes, and other secondary components (Fraenkel, 1959; Hegnauer, 1964).

*Aristolochia* swallowtails sequester some of these secondary chemicals from their hostplants, apparently making the butterflies unpalatable to

many potential predators (von Euw *et al.*, 1968; Rothschild *et al.*, 1970; Rothschild, 1972; R. Nishida, pers. comm.). The butterflies advertise their distastefulness through aposematic coloration, and serve as models in Batesian and Muellierian mimicry complexes (Rothschild & Jordan, 1906; Brower, 1958; Brower & Brower, 1964; Young, 1971a, 1971b).

Because the biology of the troidine swallowtails is linked so closely to that of their *Aristolochia* hostplants, a thorough study of this plant-insect association could provide insights into the evolution of plant defenses, and into the use of plant chemicals by insects. The basic biology of the system has received limited attention until recently. Several studies of the natural history of various North and Central American troidines have appeared in the past decade (Young, 1971a, 1971b, 1972a, 1972b, 1973, 1977, 1979; Muyschondt, 1974; Rausher, 1979a, 1979b; de Vries, 1979). Rausher (1979a) studied the interaction of *Battus philenor* and its two host plants in southeastern Texas. The South American members of the tribe have been studied by Moss (1919), D'Almeida (1922, 1944, 1966), and Cook *et al.* (1971).

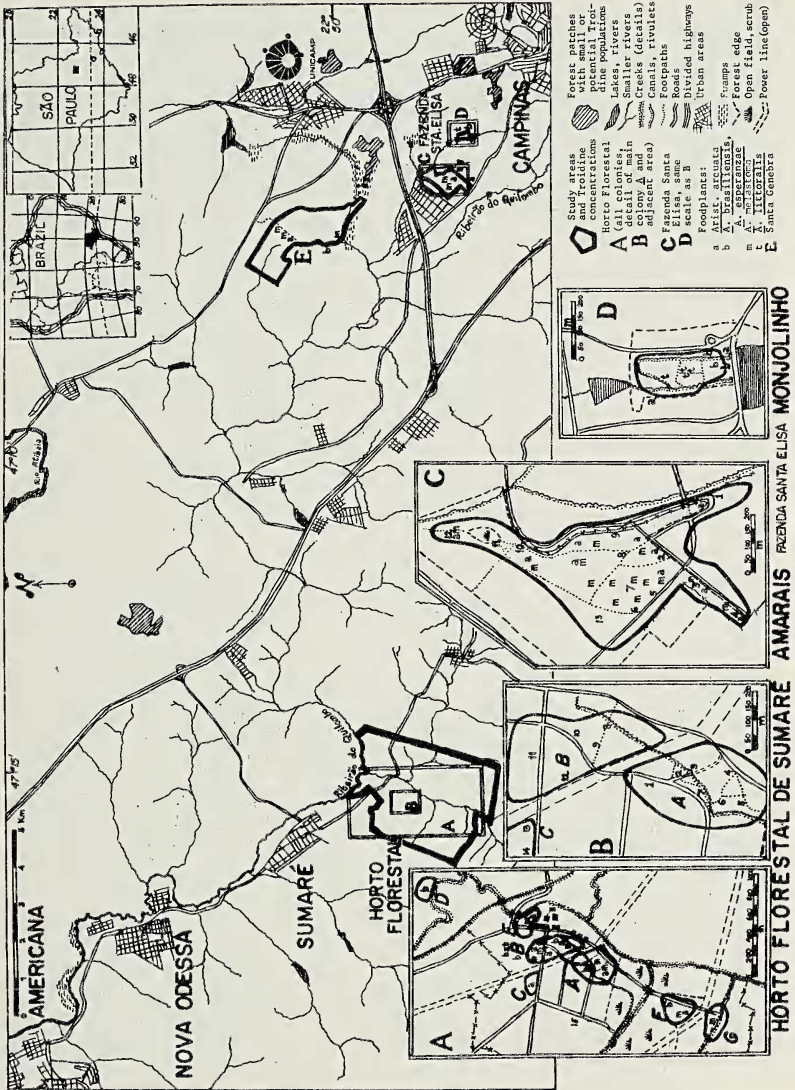
In this paper we describe an assemblage of five troidine butterflies sympatric in central São Paulo state (*Battus polydamas*, *Parides proneus*, *P. bunichus*, *P. agavus*, *P. anchises nephalion*<sup>3</sup>), emphasizing the interaction with their *Aristolochia* hostplants. The natural histories and laboratory culture techniques presented here provide the foundation for planned field and laboratory studies of the biological and chemical aspects of this Troidini-*Aristolochia* interaction.

### Study Sites and Methods

Wild troidine populations were observed on the grounds of the Horto Florestal de Sumaré, located in the interior of the state of São Paulo, Brazil (22°51'S., 47°16'W., 600 m elevation) (Figure 1, A and B). Between October and March (summer), temperatures at Sumaré average 23°C; the April to September (winter) average is 18.5°C and daily temperature ranges often exceed 10°C. The bulk of the average annual rainfall of 1300 mm falls during the summer. Because Sumaré lies at the intersection of three major climatic domains, the distribution of the annual precipitation is highly variable from year to year (Figure 2).

The Horto Florestal (856 ha, of which 50 were intensively covered in the field work) covers a mosaic of poor, sandy soils and rich soils, originally supporting cerrado scrub and semi-deciduous open forest, respectively. The troidines inhabit riverine tangles and the shady middle and understory beneath an introduced *Eucalyptus* canopy of the semi-deciduous forest (Figure 3). Three species of *Aristolochia*, *A. melastoma*, *A. arcuata*,

<sup>3</sup>The placement of *nephalion* and other "species" of Rothschild and Jordan (1906) as subspecies of *anchises*, and the species distributions indicated in Figure 5, follow a biosystematic revision and biogeographical study to be published by K. Brown.



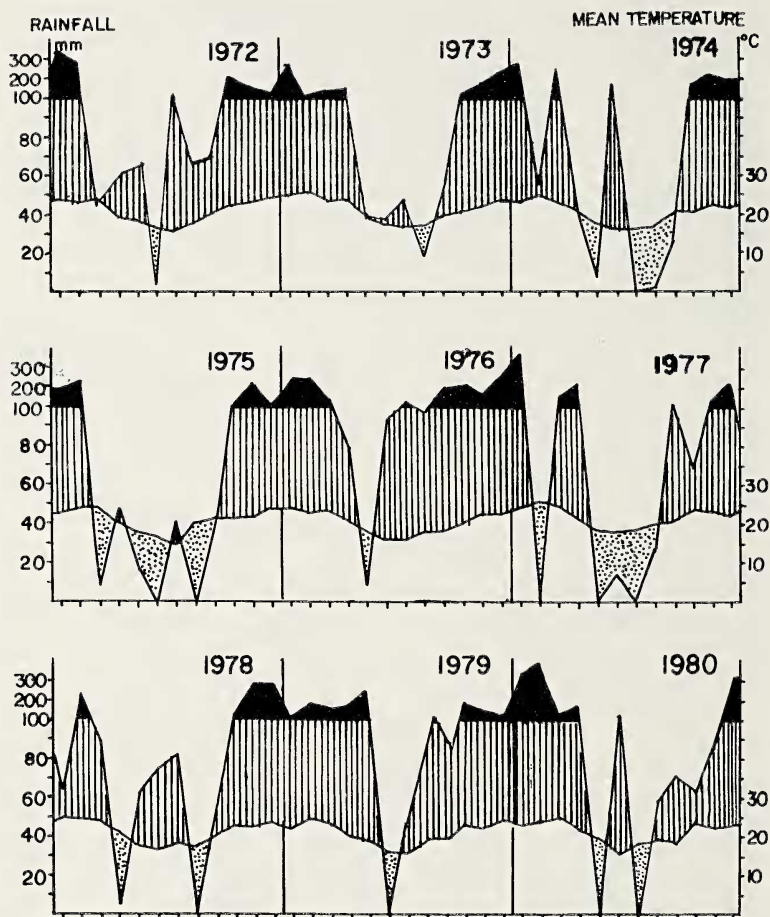


Fig. 2. Monthly and yearly fluctuations in rainfall (mm, scale at left) and temperature ( $^{\circ}\text{C}$ , scale at right) in the Horto Florestal de Sumaré, São Paulo. Data for 1974-1978 are from Vasconcellos-Neto (1980). Monthly rainfall data for 1972-1973 are from nearby Nova Odessa (see Fig. 1), other years are from within the Horto Florestal. Mean monthly temperature is corrected for altitude difference from data measured in Nova Odessa. Black areas are very humid months; dotted areas, very dry. The maximum yearly rainfall (1887 mm in 1976) immediately followed the minimum yearly rainfall for this decade (1003 in 1975).



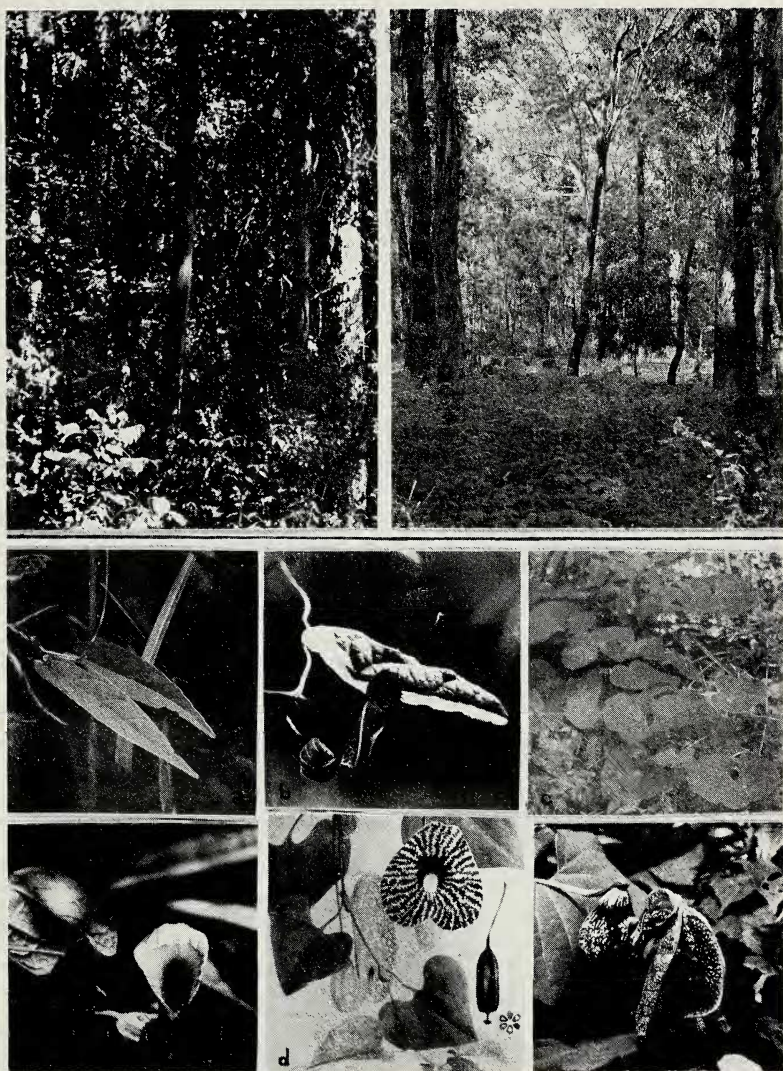


Fig. 3. Middle and understory of the *Eucalyptus* semi-deciduous forest in the (upper) Horto Florestal de Sumaré, preferred habitat of the troidines and their *Aristolochia* foodplants. Photo at right by J. Vasconcellos-Neto.

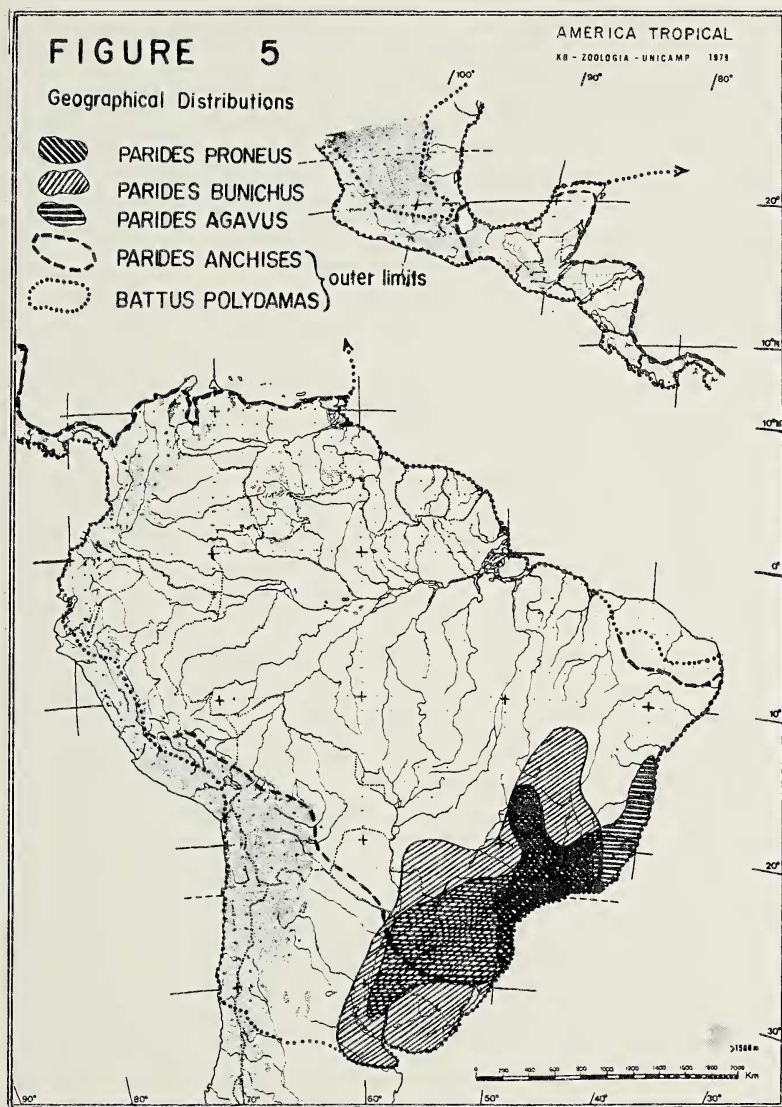
Fig. 4. *Aristolochia* foodplants of troidines, common in central São Paulo. a (left), (lower) *A. melastoma*; upper, leaves; lower, flower. b (upper center), *A. arcuata*, leaf and flower. c (right), *A. brasiliensis*; upper, leaves; lower, flower. d (lower center), *A. littoralis*, flowers, leaves and fruit, from Hoehne (1942).

and *A. brasiliensis* (Figure 4), commonly grow in light gaps, along forest edges, and in mildly disturbed areas within the forest. Two additional species, *A. littoralis* (Figure 4d) and *A. triangularis*, occur infrequently in the Horto. *A. gigantea*, cultivated nearby, represents a sixth potential foodplant for the troidine larvae.

An additional study area near Campinas, São Paulo, is the Fazenda Santa Elisa of the Instituto Agronômico de Campinas. A large troidine concentration occurs in a *Eucalyptus* woodlot similar to the Horto Florestal: Amarais, with abundant *A. melastoma* and *A. arcuata* (Figure 1, C). One km east of Amarais is the 3-ha forest garden Monjolinho (Figure 1, D), with a cool, humid understory beneath native trees; here there are patches of *A. esperanzae* (near *A. brasiliensis*) and *A. littoralis*. A fourth site, visited only occasionally, is a 250-ha woods north of Campinas (Figure 1, E) with small numbers of *A. melastoma*, *A. arcuata*, and *A. brasiliensis* plants in the more open understory and along humid edges of a natural semi-deciduous forest on rich soils. All of the study sites are in the basin of the upper Ribeirão do Quilombo (Figure 1).

The five troidines well established at Sumaré and Campinas have geographic ranges that differ widely (Figure 5<sup>3</sup>). *P. bunichus* and *P. proneus* extend into the cool montane and central plateau regions of eastern and southern Brazil, with the former much more widespread. *P. agavus* occurs most abundantly in the mild coastal regions of eastern and southern Brazil, but also extends far southward and inland. *P. anchises* and *Battus polydamas* are widespread and often prefer warm, dryer climates. At least six additional troidines are known from central São Paulo, including *Parides neophilus eurybates* which is occasionally encountered in the study sites. Observations throughout the Neotropics suggest that the occurrence of but five or six troidines out of a potential pool of 11 to 16 species at a particular site is a general phenomenon (Moss, 1919; D'Almeida, 1966; K. B., pers. obs.).

Between November 1978 and September 1979, and again after August 1980, one of us (K.B.) spent two to ten hours each week conducting mark-recapture studies of the adults in the Horto Florestal, and observing adult behavior, resource utilization, and oviposition as well as searching for larvae on the foodplants. Parallel studies were undertaken in the two Santa Elisa sites starting in the later part of 1980. Captured adults were sexed, assigned to one of six wing wear classes, numbered on the underside of each hindwing (*P. bunichus*, *P. proneus*, *P. agavus*) or forewing (*P. anchises*, *P. neophilus*, *Battus polydamas*) with an indelible marking pen ("Sharpie", Sanford Corp.), and immediately released (usually within 30 sec). Butterflies were often captured two to six times within a single sampling session (Table 1) and were invariably placed in the same wing wear class all times, attesting to the reproducibility of the wing wear assignments. Rapid return of marked butterflies to pre-capture activities









was routinely observed, suggesting relative unimportance of marking trauma.

These studies showed that the Horto Florestal harbored a 6-ha central concentration of troidines (A in Figure 1, A and B) as well as several smaller peripheral concentrations (B-G). Amarais had a single colony covering 25 ha, half of which was heavily overgrown in foodplants (Figure 1, C). Monjolinho showed rather sparse troidines in a few favored light-gaps (Figure 1, D). Populations of troidines were very sparse in the large natural woodlot north of Campinas (Figure 1, E). Troidine concentrations are infrequent within a 20-km radius of the Horto Florestal, the majority of which is dominated by fields, orange groves, and heavily populated area (Figure 1).

Laboratory cultures of butterflies were maintained in a walk-in growth chamber (Figure 6 ab) at Cornell University; stock cultures were also kept in a greenhouse (Figure 6 cd). The environment in the growth chamber approximated summer conditions in the middle and lower levels of the forest at Sumaré. A 13.5 hr "day" period faded into a 10 hr "night" period through programmed dimming of the lights over a 0.5 hr "dusk" period. Temperature alternated between a constant 26°C during the day and a constant 21°C at night. Relative humidity was kept between 85% and 90% throughout the daily cycle, but because of the constant air flow the atmosphere was a drying one. A diffuse, fine-grained, and relatively low-intensity light structure, similar to that of the Horto Florestal middle level (Figure 3), and a dark humid understory, were necessary components for the adaptation of the butterflies in both the growth chamber and the greenhouse (Figure 6). Butterflies visited cut or potted flowers as well as artificial nectar sources (consisting of an orange or yellow scouring sponge in a plastic petri dish filled with 1:6 honey:water solution). The butterflies often preferred to rest and sleep on dacron net curtains hung in the culture areas. Juvenile and adult troidines did not survive as well in the greenhouse as in the growth chamber, perhaps because of daily and seasonal fluctuations in temperature, and predation by ants. In both cultures, however, normal behavior of adults was observed (Figure 6 d-g). Individual larvae could be followed from day to day by marks on their tubercles (fourth and fifth instars) made with various colors of Liquid Paper correction fluid (Liquid Paper Corp.).

### Description of Juvenile Stages

The adult stages of most troidines are well known (Rothschild & Jordan, 1906; D'Almeida, 1966); those occurring in the study sites are illustrated in Figure 7. The juvenile stages are less well known, though larvae and pupae of most species have been illustrated or preserved. Variations in the larval characteristics of *Parides anchises*, *P. aeneas* and *P. lysander* (Moss, 1919; Young, 1977; inspection of larvae reared at Cornell University or in the field or preserved in the British Museum (Natural History) by K. B.)

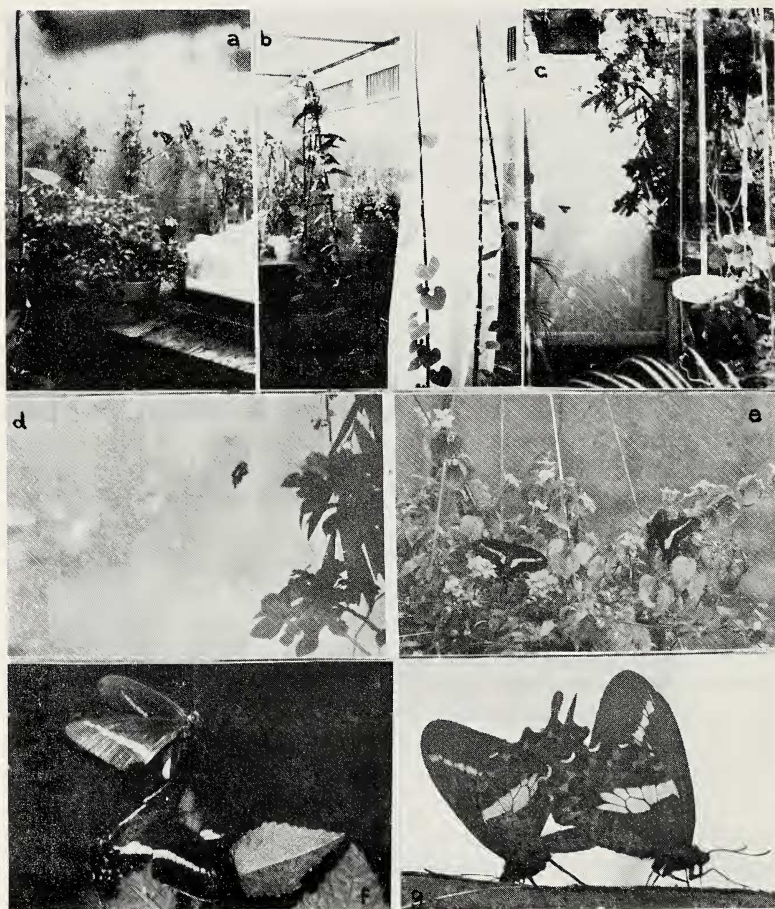


Fig. 6. Laboratory cultures of troidines in Cornell University (except for f). a-b, views of the growth chamber; in a, a *P. anchises* male is resting on a leaf at upper left, and two *P. bunichus* are on flowers at the rear, by plastic boxes used for pupal experiments. c-d, views in the greenhouse; in c, a *P. bunichus* is flying at the rear, and in d, another one is approaching an *Impatiens* flower. Note the light structure (diffuse in middlestory, dark in understory) in a-c, and Dacron net curtains in b-d. e, a *P. bunichus* and a *P. proneus* on *Lantana* flowers in the growth chamber. f, a courtship of *P. bunichus* (near Campinas, São Paulo; photo by I. Sazima); note the exposed white scent pouch of the male hindwing over the female antennae. g, a copula of *P. bunichus* in the greenhouse; both male and female had eclosed from the pupa earlier on the same day.

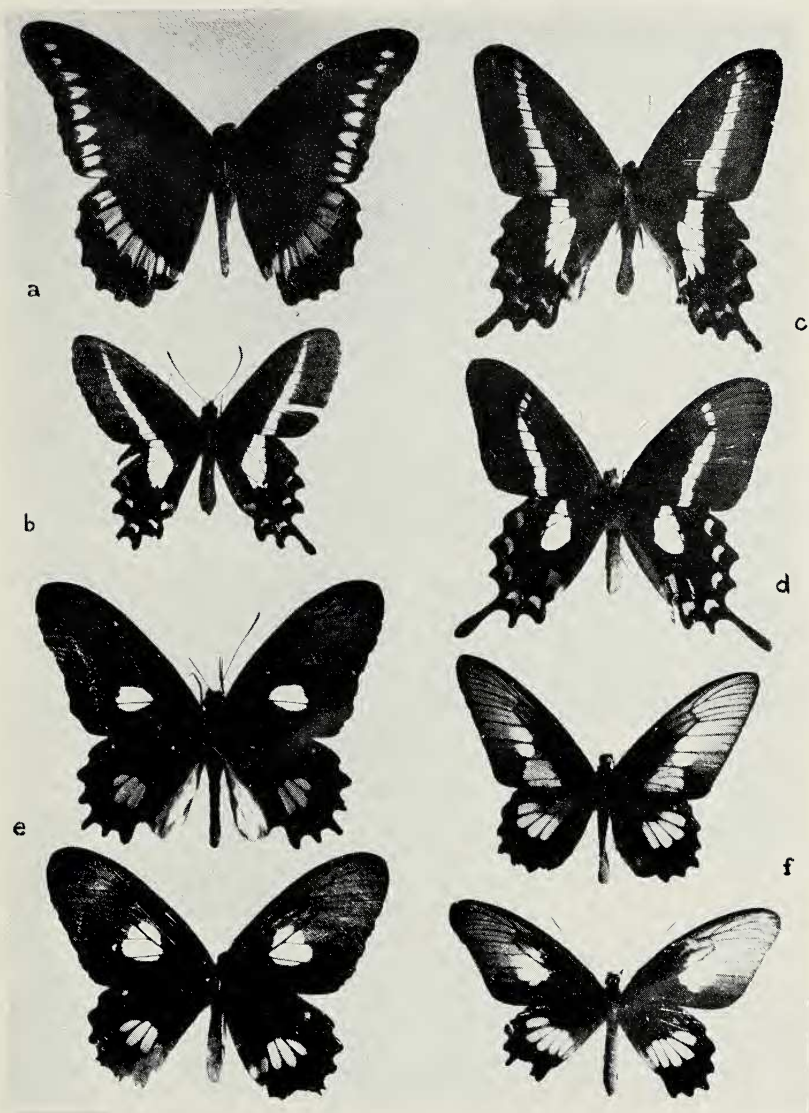


Fig. 7. Adults of troidines captured in the Horto Florestal de Sumaré. a, *Battus polydamas*, male; b, *Parides proneus*, female; c, *P. bunicuss*, male; d, *P. agavus*, female; e, *P. anchises nephalion*, male (upper) and female (lower); f, *P. neophilus eurybates*, male (upper) and female (lower). Note the white or black androconial scales in the male *Parides* hindwing anal folds (c, and e-f upper).



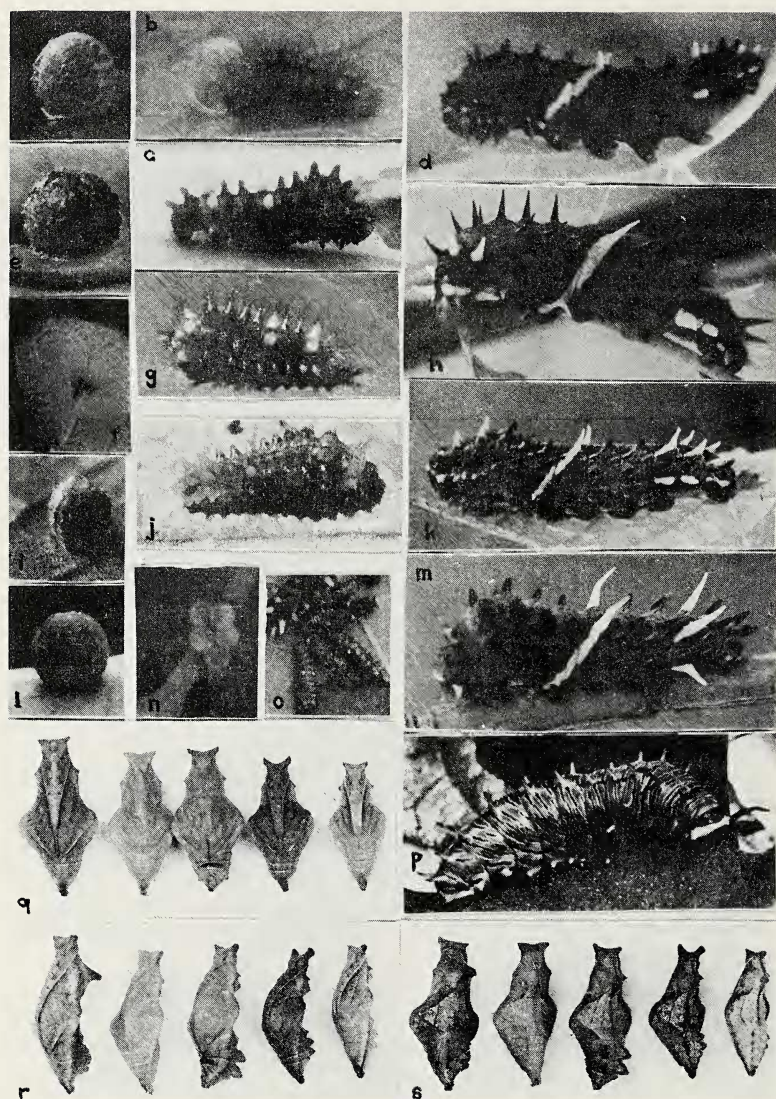


Fig. 8. Juvenile stages of the five resident troidines in the central São Paulo study sites. Eggs (at left) 8.5x (except for f, egg position under leaf, 1.7x; and n, egg cluster, 3.4x); first instars (left center) 7x (except for o, group of larvae, 2.3x); fifth instars (right), 1.1x; pupae (lower), 0.75x. *P. bunichus*, a-d, left center pupae; *P. anchises nephalion*, e-h, center pupae; *P. proneus*, i-k, right pupae; *P. agavus*, l-m, right center pupae; *B. polydamas*, n-p, left pupae. Pupae, q = dorsal, r = dorsolateral, s = ventrolateral.



suggest that larval color patterns may not be geographically homogeneous. Color patterns in *B. polydamas* larvae vary within a population (Moss, 1919). While it is important to briefly describe and distinguish between juvenile stages encountered in central São Paulo, the following larval color descriptions should be extended to geographically distant populations with caution.

Measurements are on organisms from laboratory cultures, which usually but not always gave normal-sized adults. Those with two significant digits to the right of the decimal were made with an ocular micrometer on material preserved in Kahle's fluid; those with only one digit were made with calipers on living organisms.

*Parides bunichus* (Huebner, 1822)

Egg (Figure 8 a): irregularly sculptured spheroid, yellow to red,  $\bar{x}$  = 1.32 mm in diameter (max. = 1.44 mm, min. = 1.19 mm, n = 89).

First instar larva (Figures 8 bc): reddish, last few abdominal segments light yellow; head capsule 0.79 mm wide (max. = 0.91, min. = 0.71, n = 165). Second instar: head capsule 1.21 mm wide (max. = 1.36, min. = 1.05, n = 75).

Third instar: head capsule 1.6 mm wide (max. = 1.9, min. = 1.4, n = 17).

Fourth instar: head capsule 2.6 mm wide (max. = 3.0, min. = 2.4, n = 31).

Fifth instar: head capsule 3.8 mm wide (max. = 4.1, min. = 3.3, n = 14).

Note non-overlap of the ranges of head capsule widths between instars, permitting unambiguous identification of larval instar.

All four *Parides* larvae share a basic pattern, with a deep maroon to dark brown-black ground color; conical, pointed, often recurved tubercles on all segments; and a light-colored, oblique side stripe from the base of a light-colored dorsolateral tubercle on the 4th abdominal segment across a light-colored subspiracular tubercle on the 3rd abdominal segment to the base of the proleg on the same. Light-colored tubercles are always present on the 7th abdominal segment (dorsolateral and subspiracular), and the 1st (dorsolateral) and 2nd (subspiracular) thoracic segments.

*P. bunichus* larvae (Figure 8 d) are distinguished by short tubercles (less than one-half head width), with the light-colored zones strong yellow to orange, and have additional light-colored dorsolateral and subspiracular tubercles on the 9th abdominal segment, but not on the 8th.

The characteristic pattern of the light abdominal tubercles (segments 7-9) of this species and the following three can be recognized in most individuals by the late first instar, and permits rapid and unambiguous identification of larvae.

Pupa (Figure 8 qrs, second from left): light brown or green, short cephalic projections, no abdominal flanges, two dorsolateral maroon dots on the 1st abdominal segment.

*Parides anchises nephalion* (Godart, 1819)

Egg (Figure 8 ef): pinkish-yellow, noticeably lighter in color and larger than that of *P. bunichus* (diam. = 1.4-1.5 mm).

First instar (Figure 8 g): similar to *P. bunichus*. Head capsule about 0.8 mm wide (n = 3).

Second instar: head capsule 1.3 mm wide (max. = 1.4, min. = 1.1, n = 20).

Third instar: head capsule 1.8 mm wide (max. = 2.0, min. = 1.6, n = 30).

Fourth instar: head capsule 2.7 mm wide (max. = 3.0, min. = 2.3, n = 8).

Fifth instar: head capsule 4.1 mm wide (max. = 4.9, min. = 3.5, n = 7).

Note the larger width of the head capsule in all stages of *P. anchises* in relation to *P. bunichus*.

Light colored areas pale yellow; distinguished by additional light dorso-lateral and subspiracular tubercles on the 9th abdominal segment, and subspiracular tubercles on the 8th and usually all thoracic segments, producing prominent yellow lateral patches at the front and rear ends of the larva. All tubercles are nearly as long as the head capsule width, and twice as long as those in *P. bunichus*.

Pupa (Figure 8 qrs, center): green and yellow (brown phase not observed in southern Brazilian populations), moderate cephalic projections, long spatulate flanges on 6th and 7th abdominal segments, upper abdomen widely flaring.

According to Moss (1919), the larva of *P. neophilus eurybates* (Gray, 1852), which should be found occasionally in the study sites, is nearly identical to that of *P. anchises nephalion*.

Details of head capsule width for each instar are not available for the remaining species, described below.

*Parides proneus* (Huebner, 1825)

Egg (Figure 8 i): grayish-white and small (diameter  $\approx$  1.0 mm).

First instar (Figure 8 j): very yellowish in the posterior abdominal segments; strongly club-shaped, with an expanded thorax, tapering posteriorly.

Fifth instar (Figure 8 k): distinguished by additional light yellow dorso-lateral and subspiracular tubercles on both the 8th and 9th abdominal segments and on the 3rd thoracic segment. Most tubercles short as in *P. bunichus*, but light-colored tubercles twice as long. Ground color strongly striated with light gray.

Pupa (Figure 8 qrs, right): green or light brown and yellow, moderate cephalic projections, short flanges on 5th through 7th abdominal segments.

*Parides agavus* (Drury, 1782)

Egg (Figure 8 l): usually darker red than that of *P. bunichus*, but similar in size.

First instar: similar to that of *P. proneus*, likewise rather club-shaped; less yellowed posteriorly.

Fifth instar (Figure 8 m): distinguished by additional light-colored subspiracular tubercles on the 2nd thoracic segment and the 9th abdominal segment, but not the dorsolateral tubercles on the 9th abdominal segment; light-colored abdominal tubercles twice as long as other tubercles. Ground color often mottled with lighter streaks. Somewhat club-shaped as in *P. proneus*.

Pupa (Figure 8 qrs, second from right): long narrow cephalic projections, triangular flanges on 6th and 7th abdominal segments, red antenna cases, otherwise green or beige strongly mottled with yellow.

*Battus polydamas* (Linnaeus, 1758)

Egg (Figure 8 n): relatively smooth and small (diameter = 1.0 mm), and deposited in clusters (unlike *Parides* eggs which are always laid singly), usually 2 to 9.

First instar (Figure 8 o): yellow, turning to brown with lighter tubercles after one or two days.

Second to fourth instars: tending to dark red or brown with subequal wire-like tubercles, lighter on the 2nd thoracic and fourth and seventh abdominal segments, thus at times superficially similar to some *Parides* larvae, especially in earlier instars.

Fifth instar (Figure 8 p): wire-like subequal tubercles on all segments, except for dorsolateral tubercles on first thoracic segment and subspiracular tubercles on 2nd (usually) and 7th abdominal segments which are much longer (from the second instar, permitting unambiguous identification). Body maroon, grey, or beige in various proportions, striated with lighter or darker markings, especially late in the instar.

Tubercles the same color as body or lighter, occasionally bicolored.

Pupa (Figure 8 qrs, left): green or light brown and yellow, with a long spatulate dorsal process on the thorax (present in all *Battus*, never seen in *Parides*; Moss, 1919).

### Adult Biology

In the laboratory, adults of all species eclosed in the morning (see also Moss, 1919), and were actively flying by midday and for one to two weeks thereafter. In the field, butterflies were rarely recaptured more than two weeks after marking, and consistently passed through one of the six major wing wear classes per week (Table 1, Figure 9). A maximum of 35 days between first marking and last recapture was recorded for a male of *P. proneus* and a male of *P. bunichus*; two males of *P. agavus* lasted 49 and 56 days in Monjolinho, a cool, humid and protective environment with abundant adult resources in the understory. In the growth chamber, lifespans of *P. bunichus* averaged 11.4 days (max. 24 days,  $n = 47$ ), in general agreement with the field data. These results approximate those obtained for troidines in Trinidad forests by Cook *et al.* (1971) and in Texas thickets by Rausher (1979a), but contrast markedly with the 2 to 7

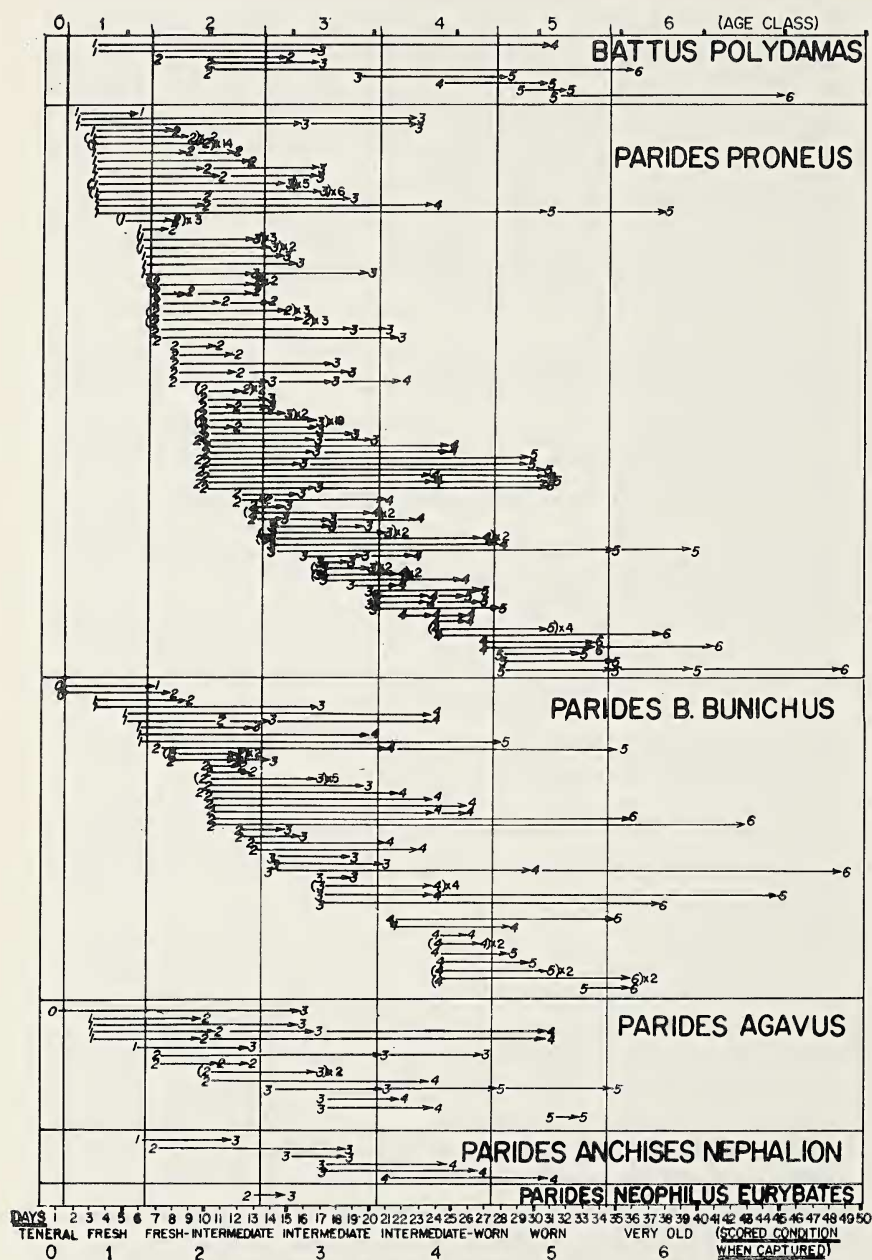




Fig. 9. Aging of recaptured troidines, combined field sites (1980): test of the hypothesis of passage through one of the six wing wear classes each week. Recapture lines for individually numbered butterflies always start within the scored wear class at first marking. Of 61 butterflies which should be in class 2 (fresh-intermediate) when recaptured, 53 in fact were, with 1 in class 1 and 7 in class 3. For recaptures in the other classes of wing wear, 3 shows 89 in 3, 9 in 2, and 3 in 4; 4 shows 44 in 4, 10 in 3, and 3 in 5; 5 shows 20 in 5, 8 in 4, and 3 in 6; and 6 shows 13 in 6 and 9 in 5. Maximum inferred lifespan was 49 days in two separate cases. Note that butterflies were placed at various points within their wing wear class as scored on first capture, in accord with recapture data. If all individuals are placed only on the midpoint of their wing-wear class upon first recapture, and seven days are allotted to each class (except for teneral = 1 day and fresh = 6 days), the numbers found in each recapture set, including all data through early August 1981, are as follows:

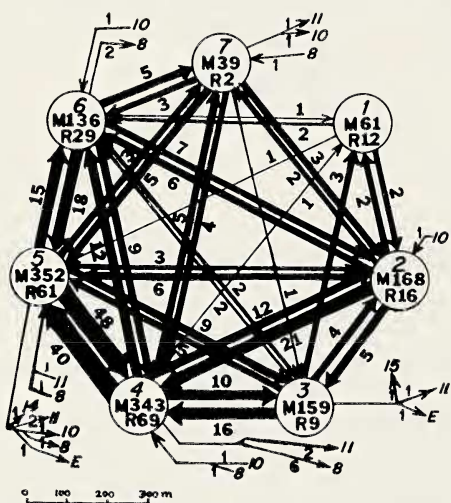
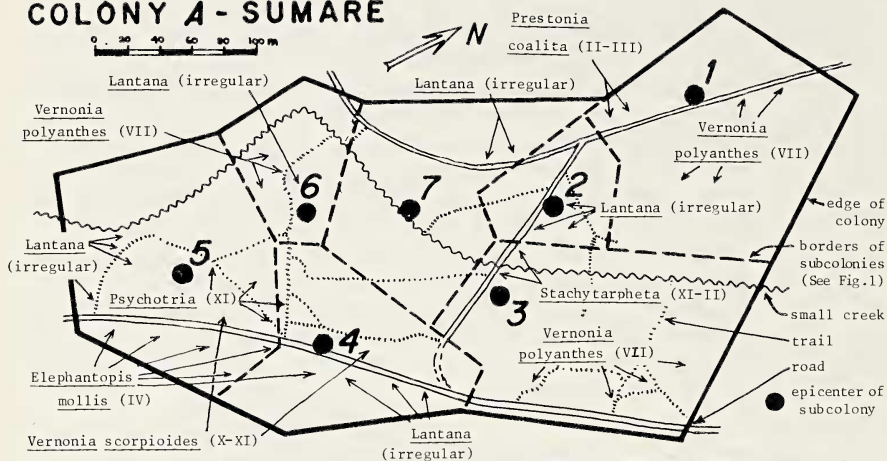
Predicted Class upon Recapture	Total Number of Recaptures	Number Found in Each Wing Wear Class, As Actually Scored Upon Recapture					
		1	2	3	4	5	6
1	3	<u>3</u>					
2	101	4	<u>71</u>	26			
3	139		21	<u>107</u>	11		
4	91			<u>25</u>	<u>59</u>	7	
5	67			3	21	<u>36</u>	7
6	<u>42</u>				3	<u>20</u>	<u>19</u>
	443						

It may be noted that aging is somewhat accelerated (with relation to the hypothesis) in the earlier wing wear classes, and somewhat retarded in the three later classes, but the overall picture is very coherent.

month lifespans reported by Young (1971a, 1971b, 1972a, 1972b) for wild and captive adults in Costa Rica.

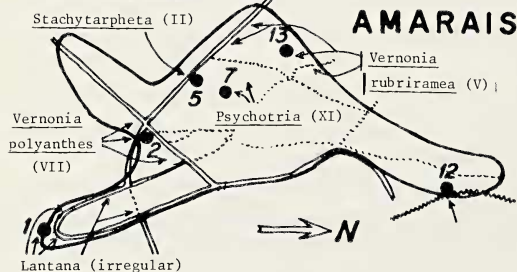
The mark-recapture studies indicated that butterflies rarely moved between the main colony of the Horto Florestal (A in Figure 1 AB) and the outlying concentrations, but often moved around all parts of Area A (Figure 10). In 1980, males captured in the Horto Florestal colony A moved an average of 81 m and a maximum of 660 m between successive captures on the same day ( $n = 158$ ), or 116 m (average) and 970 m (maximum) on different days ( $n = 135$ ) (distances were represented by minimum straight-line paths between epicenters of marking areas; see Figures 1 and 10). Corresponding values for females were very similar: 77 m (average) and 620 m (maximum) for the same day ( $n = 55$ ), and 110 m and 490 m for different days ( $n = 30$ ). Some evidence for dispersal over several hundred meters or across major barriers emerged from the data, especially in periods of sparse or ephemeral adult resources. Between colony recaptures (A to B or E) numbered only 31 in the total of 825 recaptures, however (Table 1, Figure 10). The occasional appearance in

## COLONY A - SUMARÉ



AREAS, DATES AND CAPTURES (in area/total)

1	2	3	4 + 5	6	7
19-I	4-I	15/35			11-I
19/43			7-II	21/35	14-II
					23/48
26-II	17/27				20/48
5-III	13/19		21-III	63/69	
			24-III	54/61	
			31-III	48/67	
			7-IV	26/27	
			27-VI		28-VII 10/22
			12/21		4-VIII 17/32
20-VIII			1, 3-IX	46/67	7-VIII 10/24
25/55			10-IX	42/102	
			24-IX	71/106	17-IX 38/97
			1-X	57/87	
			15-X	59/74	
22-X			20-X	22/28	
22/50			5-XI	39/60	
			12-XI	64/77	
			19-XI	42/56	
			22-XI	21/31	
23-XI			21/44	26-XI 46/51	
30-XI	20/40				14-XII
					14/30
22-XII	13/27				
28-XII	27/46				



## AMARAIS

1	2	5	7	13	12
			19-II		
			16/32		
7-III	16/33				
12-III	14/31				19-III
					13/29
2-IV	18/37				
6-IV	12/23				
16-IV	17/35				
23-IV	8/15				30-IV 6/13
					15-V 79/86
					19-V 38/40
					21-V 9/11
27-VII	25/28				
30-VII	55/67				
6-VIII	19/43				
					VI-high
					Eucalyptus flowers
8-XI	44/56				
					11-XI 55/75
					18-XI 61/87
					27-XI 42/62

Fig. 10. Movement of adult troidines, and relationship of population concentrations with seasonal nectar sources in Colony A of the Horto Florestal de Sumare (above) and in the Amarais woods (below) (see Figure 11). Locations of preferred flowers, which attracted exceptional densities of Troidines, are indicated on the base maps of each area, along with the epicenters for captures in each subcolony (dark circles). At left center is a summary of all marks and recaptures in the Horto Colony A (as a schematized heptagon), by subcolony (circles at apices); M = total number marked in the subcolony, R = total number of first subsequent recaptures, and numbers by each arrow = first subsequent recaptures in other subcolonies; external arrows = subsequent recaptures or prior captures outside Colony A, representing intercolony transfers. At right are graphs showing movements of populations between different subcolonies throughout the year (Horto Colony A above, Amarais below), giving respective dates, number of captures in the indicated subcolony, and total number of captures for that date; for example, on March 31, 1981, 48 of the 67 troidines captured in Horto Colony A were on *Elephantopus* flowers in subcolonies 4-5; on February 19, 1981, half of the 32 troidines captured in Amarais were on *Stachytarpheta* flowers in subcolony 5. All subcolonies were always covered in each day's sampling, usually several times, but more time was spent in areas where more butterflies were encountered. Dotted arrows indicate discontinuities (different years of observation; refer to Figure 11).

the Horto Florestal of *P. neophilus eurybates*, apparently not a resident there, suggests that immigration and emigration of the resident species could occur, in spite of the unfavorable habitat extending on all sides of the site (Figure 1). In support of this, a male *P. agavus* marked in the riverside thicket D (Figure 1A) was captured a week later within the Horto Florestal colony E, one km to the SW. In the more continuous habitat of the Amarais forest (Figure 1C), individual movements of over 400 m between the scattered flower patches were more frequently recorded (23% of all recaptures). One *agavus* male flew from Amarais to Monjolinho (about 1.3 km) in an hour and a half; a female *bunichus* was also captured in Monjolinho two weeks after being marked in Amarais; and a female *agavus* and a male *proneus* marked in Monjolinho were captured in Amarais, 7 and 32 days later, respectively.

The short life spans of the adults precluded the use of standard methods (Jolly-Seber, Lincoln-Bailey, Manly-Parr) for estimation of population sizes from weekly samples; most butterflies were not recaptured, and very few were recaptured twice (Figure 9). When several samples were made at 2-day intervals, a simple Lincoln analysis suggested that about a third of the *P. proneus* population, a fourth of the *P. bunichus* population, and a tenth of the *B. polydamas* population of Horto Florestal colony A was being marked or sampled in a 4-hr standardized intensive capture period (other species gave less than five recaptures). In Figure 11, all samples are

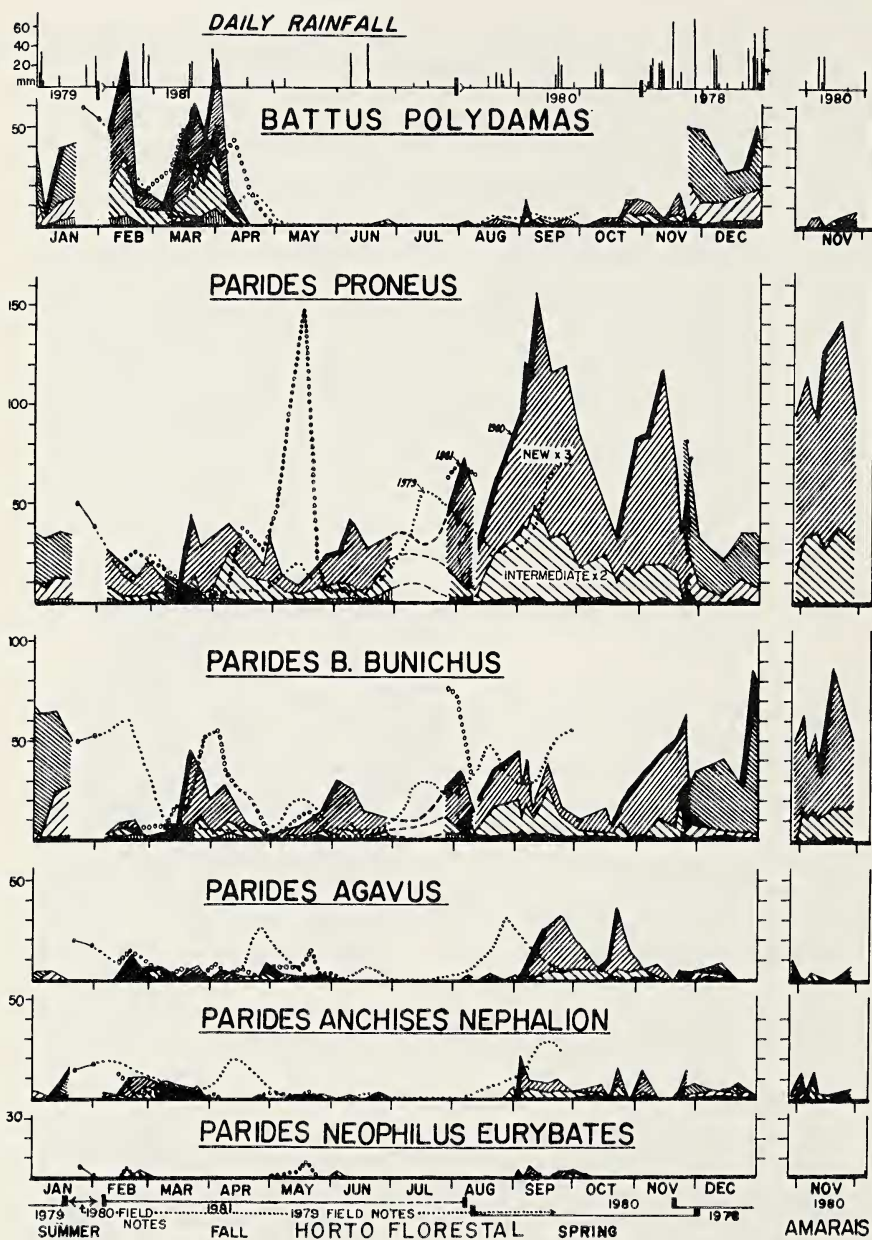




Fig. 11. Variation during the year in relative abundance of troidines in the main colony A of the Horto Florestal de Sumaré, from field data, 1978-1981. All numbers are adjusted to a four-hour sampling period. The daily data have been exaggerated to better define brood emergences - fresh individuals (wear classes 0-2) are given triple their value, intermediate ones (wear classes 3-4) double. Dotted lines are based on numbers seen or captured in weekly visits outside the disciplined mark-recapture periods. Data from Amarais, November 1980 is presented at right for comparison; uppermost curves for Amarais populations are also shown as chains of open circles on the Horto graph, for February to August 1981. Note non-successive broods (less than two months interval) in *B. polydamas*, *P. bunichus*, *P. agavus*, and *P. a. nephalion*; non-overlap of 1978 and 1980 (November), 1979-1981 (February through early August), and 1979 and 1980 (August and September) data; and desynchronized broods of *P. agavus* and *P. a. nephalion* in relation to the commoner species.

corrected to 4 hr, and more weight is given to younger age classes in daily samples; in this way, a very approximate picture of brood emergences and monthly and yearly population fluctuations can be obtained.

Concentrations of butterflies were invariably encountered on the most abundant flower resources within the colony areas (see Figure 10). Adults fed exclusively on nectar, in the field and in the laboratory. Pollen feeding (cf. de Vries, 1979) was not observed in central São Paulo or in any other parts of the Neotropics. "Puddling", common in the *Graphium* mimics of troidines and thus often reported for this tribe, has only been observed occasionally for *Battus*, never for *Parides*. In the Horto Florestal and Amarais, butterflies visited *Lantana camara* L. and *L. lilacina* Desf. (Verbenaceae) flowers throughout the year. Seasonal nectar sources included *Petrea racemosa* Nees et Mart. (late winter) and *Stachytarpheta polyura* Schau. (spring and summer) (also Verbenaceae), *Psychotria* and *Palicourea* species in late spring (Rubiaceae), *Vochysia tucanorum* Mart. (Vochysiaceae) and *Prestonia coalita* (Vell.) Woods. (Apocynaceae) in late summer, and *Vernonia rubriramea* Mart., *V. scorpioides* Pers., and other composites in the fall and winter. The principal nectar source in Monjolinho was introduced *Impatiens* (Balsaminaceae), abundant in the understory, supplemented by *Lantana*, *Ixora*, *Euphorbia*, and other ornamental flowers in the adjacent sunny garden (exclusive habitat for *B. polydamas*). When nectar sources dwindled in number, especially in fall and winter, butterflies were recaptured far from their marking localities, and males became increasingly protective of the flower patches, attempting to expel other males which appeared near them. Males often courted the females near the flower concentrations. During courtship, males hovered over females, occasionally darting to and fro, and appearing to brush the white androconial scales on the dorsal surface of the anal fold of the hindwing against the antennae and head of the female (Figure 6 f).

TABLE 2  
CHOICE OF OVIPOSITION SITES BY THE TROIDINES RESIDENT IN SUMARE<sup>1,2</sup>

Butterfly Species	melastoma		arcuata		Aristolochia species used			
	field	lab	field	lab	triangularis	brasilensis	littoralis	gigantea
	field	lab	field	lab	field	lab	field	lab
<i>Battus polydamas</i>	x	x	x	x	?	x (x)	x	x
<i>Parides proneus</i>	x	x	(x)	x	?	o	o (x)	?
<i>P. buniachus</i>	x	x	x	x	x	o	x	x
<i>P. agavus</i>	x	x	x	x	?	x	?	o
<i>P. a. nephallion</i>	x	x	x	x	?	x	x	x

<sup>1</sup>Plants and insects are in probable evolutionary progression (more advanced to right or below). (Hoehne, 1942; Borwn, in prep.)

<sup>2</sup>x = oviposits frequently, (x) = oviposits occasionally, o = does not oviposit, ? = unknown.

TABLE 3  
COMPARISON OF THE RESPONSES OF TROIDINE LARVAE TO DIFFERENT ARISTOLOCHIA SPECIES IN THE FIELD AND UNDER LABORATORY CONDITIONS<sup>1</sup>

Butterfly Species	melastoma		arcuata		Aristolochia species fed upon			
	field	lab	field	lab	triangularis	brasilensis	littoralis	gigantea
	field	lab	field	lab	field	lab	field	lab
<i>Battus polydamas</i>	3	x	3	x	?	x	2 (x)	3
<i>Parides proneus</i>	3	x	1	x	?	x	o	o
<i>P. buniachus</i>	3	x	3	x	?	x	o (x)	?
<i>P. agavus</i>	2	x	2	x	?	x	?	x
<i>P. a. nephallion</i>	3	x	3	x	?	x	2	x

<sup>1</sup>x = develops well, (x) = develops slowly with increased mortality, o = very poor development, high mortality, 0-3 = increasing utilization of plant in the field, ? = not known or observed.

<sup>2</sup>principally on flowers

Laboratory observations indicated that both males and females could mate on the day of eclosion (Figure 6 g). Virgin females up to two weeks old could mate and subsequently laid fertile eggs; before mating, females very rarely laid (infertile) eggs. The female copulatory pore is internally plugged by sclerotic bars after mating, so multiple matings are very unlikely.

When all captures and recaptures (3571 to mid-1981; Table 1) were plotted by species and sex against half-hour time intervals from sunrise to sunset, females of all *Parides* species were seen to predominate over males in the earliest and latest hours of the day, while the opposite was true for *Battus* (females flew mostly near midday). *Parides proneus* was active significantly earlier in the day than the other species (peaking from 9-10 AM; *polydamas* peaked near 11 and the other *Parides* species showed near-constant activity from 10 AM to 2:30 PM).

## Oviposition and Larval Biology

*Parides* females deposited eggs singly, usually on the underside of leaves (Figure 8 f). *Battus*, on the other hand, placed eggs in small clusters on the growing tips of the *Aristolochia* vines (Figure 8 n). Females of all five species preferred some species of *Aristolochia* over others when choosing oviposition sites, possibly using chemical cues to identify the preferred species (Table 2). Prior to oviposition the females appeared to inspect the vines visually before "drumming" the leaf surface with their foretarsi. The selection of suitable oviposition sites in the field seemed to depend, also, on the habitat in which the *Aristolochias* grew; *P. anchises nephalion* often oviposited in drier portions of the Horto Florestal (C and F, Figure 1A), while *Battus polydamas* appeared to prefer open habitats (see also Rausher, 1979b) and *P. proneus* invariably favored low plants, essentially always *A. melastoma*, in dense undergrowth.

Observations of *P. bunichus* in the growth chamber indicated that females deposited about 20 eggs per day and could continue to produce eggs for up to ten days following the first oviposition. *Parides* females did not oviposit as exclusively on apical leaves as did *Battus* females. *A. littoralis*, *A. gigantea*, and *A. arcuata* leaves often formed necrotic zones where the egg contacted the leaf, similar to that illustrated under a *Parides photinus* egg by Ross (1964). These areas occasionally fell from the leaf, taking the egg with them.

Eggs of *Parides* had an irregular, hard coating deposited on them by the female at the time of oviposition. This coating was poorly developed in *B. polydamas*. Five to eight days after oviposition the larvae hatched, eating the egg shell and its coating. Young (1973) proposed that such coatings contained chemicals that protected the egg. Moss (1919) and L. E. Gilbert (pers. comm. to K. B.) suggested that the coating might contain energy rich nutrients to fuel the newly hatched larvae as they sought out the tender apical leaves on which they prefer to feed. By the late second, or early third instar, the larvae could move onto older, tougher leaves. The solitary habit of *Parides* larvae, coupled with their tendency to eat any unhatched eggs and attack smaller larvae that they encountered, limited the damage inflicted on a plant. *B. polydamas* larvae were gregarious, displaying no cannibalistic tendencies, and remained several to a plant even after the third instar. Consequently, they did much damage to the *Aristolochia* plant under attack (cf. Moss, 1919). All mature *Aristolochias* except *A. melastoma*, which had little storage root, quickly sent out new shoots when eaten back to the ground, so that defoliation was generally not fatal to the plant. Seedlings and small plants, however, might be killed more easily by extensive herbivory (Rausher and Feeny, 1980).

## Larvae-Aristolochia Interactions

The laboratory studies showed that larvae of all five species could develop in 20 to 30 days, agreeing with reports of Moss (1919) and Young



(1971a, 1973, 1977) for various species of *Battus* and *Parides*. Developmental rates of the larvae depended greatly on the species of *Aristolochia* on which they fed (Table 3). Most larvae developed rapidly on *A. arcuata* and *A. melastoma*, and poorly on *A. brasiliensis* and *A. gigantea*. *A. littoralis* seemed to be of intermediate quality (see also Young, 1973). *P. proneus* larvae seemed to be the most specialized, growing rapidly only on *A. melastoma*, while *B. polydamas* could eat and develop well on most *Aristolochias* available to it. *P. anchises nephalion* survived better on *A. brasiliensis* (which it uses in the field in Sumaré) than the other butterfly species, and *P. agavus* seemed the best adapted to *A. littoralis* (and even *A. gigantea*). The patterns of hostplant palatability roughly paralleled patterns of preference for oviposition site (Table 2), and helped to explain the near absence of *P. proneus* and the predominance of *P. agavus* in Monjolinho (Table 1).

In the field, larvae occurred on a limited subset of the palatable *Aristolochia* species available to them (Table 3). The limited use of some food plants that would support larval growth could have resulted from the inability of females to locate or recognize these plants in the field, from unsuitable microclimatic conditions on these plant species linked to differences in the sites in which the *Aristolochias* grew, or from physical or biological conditions external to the troidine-*Aristolochia* system that influence hostplant palatability.

### Pupal Biology

The larvae entered a wandering stage prior to pupation. Even at high hostplant densities, such as those in the growth chamber, larvae frequently selected pupation sites other than *Aristolochia* plants. Butterflies normally eclosed after 13 to 17 days as pupae. Many *P. bunicus*, and some *P. proneus* and *P. agavus* larvae that developed in the drying atmosphere of the growth chamber went into diapause as pupae. *P. anchises* and *B. polydamas* never entered diapause under these conditions. Diapause in *P. bunicus* lasted up to 115 days, and was characterized by a loss of 0.05% to 0.5% of total pupal weight per day compared to a loss of 1% to 3% of total pupal weight per day in non-diapause pupae. Most diapausing *bunicus* pupae broke diapause within two weeks of transferral to closed plastic boxes lined with moist paper toweling, suggesting that humidity plays an important role in diapause control in this species. D'Almeida (1966) reported that *B. polydamas*, *P. anchises nephalion*, *P. agavus*, and many other species in Rio de Janeiro usually skipped winter generations. Perhaps in these species, diapause is cold-induced.

Pupal diapause would enable butterflies to escape the unfavorable weather and limited flower abundance of cold or dry winters, factors that appeared to influence the phenology of the troidines at Sumaré (Figure 11). All five troidines were present in the spring and summer, when as many as 250 individuals could be seen in a single day. Some staggering of

brood emergences was verified in this period, perhaps related to the shared foodplants (Tables 2 and 3), the short adult lifespan (Figure 9), the long juvenile development time, and varying responses of diapausing pupae to rainy spells (Figure 11). Only *P. bunichus* and *P. proneus* persisted through the winter months, though both were scarce at times from March to May (Figure 11), when *P. agavus* and *P. anchises nephalion* were more frequent. *B. polydamas* was nearly absent during the cooler half of the year, and increased very slowly in the dry spring of 1980 (Figure 11). D'Almeida (1966) observed that troidines occurring together in the vicinity of Rio de Janeiro had staggered peaks of emergence. Foodplant phenology may also influence the feeding patterns of the troidines. *A. arcuata* and *A. melastoma* initiate most of their new growth in winter when most butterfly populations are at a low ebb (Figure 11).

### Concluding Comments

Several interactions may define the relationship of *Parides* and *Battus* to their *Aristolochias* hostplants in southeastern Brazil. The chemistry of the *Aristolochias* could act to influence the patterns of damage by the troidines, and also to allow the troidines to identify some of them as suitable hostplants. Disproportionate levels of parasitism and predation on any of the *Aristolochias* could reduce larval survival on those plants, even were the plants to be intrinsically suitable as food. The spectrum of *Aristolochias* used by a troidine species might be limited by competition with other troidines. The physical environment could restrict the *Aristolochias* available to a troidine on a spatial or seasonal basis. The evolutionary history of each of the five species could influence the pattern of hostplant utilization directly by limiting the hostplant characteristics to which they have adjusted and indirectly by limiting environments in which each troidine can survive.

The larvae of the five troidines at Sumaré did not grow equally well on all the *Aristolochias* available to them when reared under identical conditions in the laboratory (Table 3). Similarly, the females would not oviposit equally on the six available *Aristolochias* (Table 2). In both cases plant chemistry is implicated. Not all *Aristolochias* that supported growth of the larvae of a troidine species were used by that butterfly in the field, however, indicating that plant chemistry is not the only factor in play. Because of the seasonal variation in the abundance of the swallowtail species and in the phenology of growth in some of the *Aristolochias*, the presence of tender foliage suitable for consumption by first instar larvae on an *Aristolochia* that was otherwise palatable did not always coincide with the population maxima of a particular butterfly. Only *P. bunichus* and *P. proneus* occurred in numbers during the cool winter; these two species range into the cooler montane regions, whereas the other three butterflies range into milder areas. In this way both the physical environment and the

evolutionary history of the troidines could limit the availability of some *Aristolochias* to the larvae. Parasitism and predation of larvae occurred most frequently on older leaves and on less acceptable foodplants; food quality may thus affect survival of the larvae indirectly. Competition has not been demonstrated, and indeed there is a large excess of foodplant present in Amarais and in parts of the Horto Florestal (colony A) during much of the year; the destructive feeding of *B. polydamas* larvae, however, could very well decimate smaller patches of foodplant and even affect larvae of *Parides* feeding on the same plant. Detailed experimental work on this and similar systems is necessary to answer the many questions posed by the troidine-*Aristolochia* interaction.

**Acknowledgements.** This research was made possible through support of the Universidade Estadual de Campinas, the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, Grant 74/544 - Biológicas), the Entomological Club of Oxford, and the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, Fellowship 1112.4339/78 - ZO) to K.S.B., from the National Science Foundation Grant DEB 79-22130 to P.F., and from Cornell University (A.D. White Fellowship) to A.J.D. We thank the administration of the FEPASA railroad and Sr. Pedro Levantese for permission to work in the Horto Florestal de Sumaré and Dr. R. Forster for permission to work in the Fazenda Santa Elisa. Research on larval survival in Monjolinho was assisted by I. B. Baldassari A. B. Barros de Moraes, and C. T. Teradaira. Facilities at Cornell University were provided by the Department of Entomology. Lorraine Contardo and Maureen Carter kindly assisted in tending the laboratory cultures of plants and butterflies. We thank May Berenbaum, Robert Hagen, Daniel Janzen and Jan Salick for valuable comment and discussion, and finally an anonymous referee who made several relevant suggestions.

## Literature Cited

- BERNAYS, E. A. & R. F. CHAPMAN, 1977. Deterrent chemicals as a basis of oligophagy in *Locusta migratoria*. *Ecol. Entomol.* 2: 1-18.
- BROWER, J. V. Z., 1958. Experimental studies of mimicry in some North American butterflies. II. *Battus philenor* and *Papilio troilus*, *P. polyxenes*, and *P. glaucus*. *Evolution* 12: 123-136.
- BROWER, L. P. & J. V. Z. BROWER, 1964. Birds, butterflies, and plant poisons: A study in ecological chemistry. *Zoologica N. Y.* 49: 137-159.
- BROWER, L. P., L. M. COOK & H. J. CROZE, 1967. Predator responses to artificial Batesian mimics released in a neotropical environment. *Evolution* 21: 11-23.
- COOK, L. M., K. FRANK & L. P. BROWER, 1971. Experiments on the demography of tropical butterflies. I. Survival rate and density in two species of *Parides*. *Biotropica* 3: 17-20.
- D'ALMEDIA, R. F., 1921. Notes sur quelques lépidoptères d'Amérique du Sud. *Ann. Soc. Entomol. Fr.*, 90: 57-65.
- , 1922. Mélanges Lépidoptérologiques. I. Etudes sur les Lépidoptères du Brésil. Berlin: R. Friedlander & Sohn, ix + 226 pp.
- , 1924. Les Papilionides de Rio de Janeiro. Description de deux chenilles. *Ann. Soc. Entomol. Fr.* 93: 23-30.



- \_\_\_\_\_, 1944. Estudos biológicos sobre alguns lepidópteros do Brasil. *Arq. Zool. S. Paulo* 4: 33-72, 3 pls.
- \_\_\_\_\_, 1966. *Catálogo dos Papilionidae Americanos*. Soc. Bras. de Entomologia, São Paulo, vi + 366 pp.
- D'ARAÚJO E SILVA, A. G., C. R. GONCALVES, D. M. GALVÃO, A. J. L. GONCALVES, J. GOMES, M. N. SILVA & L. de SIMONI, 1968. Quarto Catálogo dos insetos que vivem nas plantas do Brasil - seus parasitos e predadores, Parte II. Ministério da Agricultura, Rio de Janeiro, xxvi + 662, viii + 265 pp.
- DEVRIES, P. J., 1979. Pollen-feeding rainforest *Parides* and *Battus* butterflies in Costa Rica. *Biotropica* 11: 237-238.
- EHRLICH, P. R. & P. H. RAVEN, 1964. Butterflies and plants: A study in coevolution. *Evolution* 18: 586-608.
- von EUW, J., T. REICHSTEIN & M. ROTHCHILD, 1968. Aristolochic acid-I in the swallow-tail butterfly *Pachlioptera aristolochiae* (Fabr.) (Papilionidae). *Israel. J. Chem.* 6: 657-670.
- FRAENKEL, G. S., 1959. The raison d'être of secondary plant substances. *Science* 129: 1466-1470.
- HEGNAUER, R., 1964. Chemotaxonomie der Pflanzen, vol. III. Birkhäuser Verlag, Basel. pp. 184-194.
- HOEHNE, F. C., 1942. Aristolochiaceas. *Flora Brasiliensis*, 6 (XV-II). Lanzara/Instituto de Botânica, São Paulo. 141 pp., 123 pl.
- MOSS, A. M., 1919. The papilios of Pará. *Nov. Zool.* 26: 295-319, 3 pl.
- MUNROE, E., 1960. The generic classification of the Papilionidae. *Can. Entomol., Suppl.* 17: 1-51.
- MUYSHONDT, A., 1974. An unusually long pupal stage of *Battus polydamas polydamas* L. (Papilionidae). *J. Lep. Soc.* 28: 174-175.
- RAUSHER, M. D., 1979a. Coevolution in a simple plant-herbivore system. Ph.D. dissertation, Cornell University, Ithaca, New York. 240 pp.
- \_\_\_\_\_, 1979b. Larval habitat suitability and oviposition preference in three related butterflies. *Ecology* 60: 503-511.
- RAUSHER, M. D. & P. FEENY, 1980. Herbivory, plant density, and plant reproductive success: The effect of *Battus philenor* on *Aristolochia reticulata*. *Ecology* 61: 905-917.
- ROSS, G. N., 1964. Life history studies on Mexican butterflies. I. Notes on the early stages of four papilionids from Catemaco, Veracruz. *J. Res. Lep.* 3: 9-18.
- ROTHCHILD, W. & K. JORDAN, 1906. A revision of the American Papilios. *Nov. Zool.* 13: 411-752, 6 pl.
- VASCONCELLOS-NETO, J., 1980. Dinâmica de populações de Ithomiinae (Lep., Nymphalidae) em Sumaré - SP. Master's dissertation, Instituto de Biologia, Universidade Estadual de Campinas, São Paulo. vi + 206 pp.
- YOUNG, A. M., 1971a. Mimetic associations in natural populations of tropical butterflies. I. Life history and structure of a tropical dry forest breeding population of *Battus polydamas polydamas*. *Rev. Biol. Trop.* 19: 210-240.
- \_\_\_\_\_, 1971b. Mimetic associations of tropical papilionid butterflies (Lepidoptera: Papilionidae). *J. N. Y. Entomol. Soc.* 79: 210-224.
- \_\_\_\_\_, 1972a. Breeding success and survivorship in some tropical butterflies. *Oikos* 23: 318-326.
- \_\_\_\_\_, 1972b. Mimetic associations in populations of tropical butterflies. II. Mimetic interactions of *Battus polydamas* and *B. bellus*. *Biotropica* 4: 17-27.

- \_\_\_\_\_, 1973. Notes on the life cycle and natural history of *Parides arcas mylotes* (Papilionidae) in Costa Rican premontane wet forest. *Psyche* 80: 1-22.
- \_\_\_\_\_, 1977. Studies on the biology of *Parides iphidamas* (Papilionidae: Troi-dini) in Costa Ricaa. *J. Lepid. Soc.* 31: 100-108.
- \_\_\_\_\_, 1979. Oviposition of the butterfly *Battus belus varus* (Papilionidae). *J. Lep. Soc.* 33: 56-57.
-